Letters to the Editor.

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Transport of Organic Substances in Plants.

THE older writers and modern text-books affirm that the organic materials (carbohydrates, etc.) manufactured in the leaves of plants are transported downwards by means of the bast through their organs to places of consumption and storage. This belief seems to be based entirely on ringing experiments. *A priori* the bast appears to be very unsuitable for carrying out this function. Even in the most rapidly assimilating plants its cross-section is small. It is formed of short cells and comparatively short, narrow tubes, so that many cross-partitions must be traversed by the stream carrying these organic substances if they use it as a conduit. Furthermore, its resistance must be greatly increased by the fact that a large proportion of its cross-section is occupied by viscid contents—protoplasm and proteins. Evidently, in such a conduit we could only expect that velocities of transport comparable with diffusion velocities could be attained. Assuming that a 10 per cent. solution of sucrose were supplied by the leaves and that this was completely converted into an insoluble carbohydrate in a storage organ 50 cm. distant, then we might expect, after a steady state had been attained, a rate of transport, from diffusion alone, of about 2 milligrams per sq. cm. per diem. This would be equivalent to a 10 per cent. solution moving at the rate of 0·2 mm. per diem. Although this diffusion rate of transport might be somewhat accelerated by protoplasmic streaming, it is quite evident that diffusion in the bast is inadequate to account for the observed rate of transport of carbohydrates in plants. The insufficiency of diffusion to transport carbohydrates is strikingly borne out by those experiments in which cut floating leaves exposed to conditions suitable for photosynthesis accumulate carbohydrates, while only negligible quantities find their way into the water.

Close approximation to the velocity of transport in the bast, if that channel alone is used, may be obtained.

For example, a potato weighing 210 grams was attached to a stem by a slender branch about 1·6 mm. in diameter. In this branch the bast had a total cross-section of 0·422 sq. mm. This figure is a maximum, as no allowance was made for cell-walls or any non-functional element in the bast. Through this conduit, *ex hypothesi*, all the organic substance has passed during the growth of the tuber, viz. in about 100 days. According to analyses, more than 24 per cent. of the tuber is combustible; therefore we may assume that approximately 50 grams of dissolved carbohydrate has passed a conduit 0·422 sq. mm. in cross-section in 100 days. The concentration of this solution was probably not more than 10 per cent. Thus 500 c.c. of solution must have passed in 100 days, and the average rate of flow must have been 5/0·00422 cm. per diem, *i.e.* more than 1000 cm. per diem, or about 40 cm. per hour. This is evidently a much greater velocity than could be attained by diffusion in the bast, even when assisted by protoplasmic streaming.

Another way of arriving at the velocity of transport in the bast demanded by this view may be obtained from such recorded results as those of Brown and Morris on the depletion of leaves. When these results are combined with actual measurements of the total cross-section of the bast strands in the petiole we arrive at similar figures for the velocity of transport, *i.e.* if carbohydrate moves as a 10 per cent. solution the velocity of flow must be approximately 50 cm. per hour.

These considerations irresistibly force one to conclude that the cross-section of the bast is not adequate to transmit the amounts of carbohydrates actually known to travel downwards in the stems and petioles of plants. The same arguments seem to apply in ruling out the cortex as the conduit for the general transport of carbohydrates. The greater cross-section available would still be insufficient to allow the quantity transmitted by diffusion alone to account for the quantities observed.

In this connection a fact pointed out to us by Prof. Seward is of peculiar interest. In several species of tree-like Lepidodendra there is no tissue in the stem which presents the structural characteristics of bast, yet we cannot possibly assume that no transport of organic substances back from the photosynthetic organs took place in Lepidodendron.

Many observations indicate that the wood is the tissue in which this transport is effected. Hales, in 1727, published accounts of experiments showing a reversed or downward current in the stem of trees. One of us and Dr. Joly experimented with inarched branches and demonstrated a reverse current, and quite recently Ricca's brilliant work on the transport of the hormone in Mimosa renders the same phenomenon obvious (Boll. della Soc. bot. Ital., Ott., 1915, "Soluzione d'un Problema di Fisiologia," Firenze, 1916). Many observers have proved the presence of carbohydrates in the water of the tracheæ during spring, and one of us, with Dr. W. R. G. Atkins, has shown that these substances are present in a greater or less degree during the entire year (H. H. Dixon and W. R. G. Atkins, Notes from the Botanical School of Trinity College, Dublin, vol. 2, pp. 275 *et seq.*). It is only reasonable to assume that they will travel with the water current whether it moves in an upward or downward direction.[1]

Some very striking evidence for the existence of this reversed current may be obtained with plants of *Solanum tuberosum*. Thus a large potato plant was dug up from the soil with as little injury as possible to its underground stems and roots. After a short exposure to the air, but before any visible wilting had taken place, the apex of one of the leaves was cut off under a solution of eosin by means of a pair of scissors. In an hour the veins of all the leaves, the stems, and the roots were tinged with eosin. Even the roots on the far side of the tuber showed this coloration. When sections of the tuber were examined next day the strands of tracheæ in the bundles showed out with great clearness owing to their injection with eosin. This experiment was made in September.

A similar result was obtained with a specimen of *Chrysanthemum macrophyllum* left undisturbed as it grew. The tip of one of the leaves was cut off and the cut surface immersed in eosin solution at 4 p.m. on an October afternoon. Next morning the eosin was apparent in all the veins of the leaf and could be traced in the bundles of the petiole.

The transmission of clogging and poisonous substances by a reversed transpiration current has been

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[1] Lately Curtis has criticised this view, basing his attack on the results of ringing experiments. He does not, however, seem to have taken into account the blocking of the tracheæ which results from morbid changes spreading inwards through the wood parenchyma and medullary rays from the injured region. These effects have been discussed at length by Strasburger, "Leitungsbahnen in den Pflanzen."

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demonstrated by one of us (H. H. Dixon, Notes from the Botanical School of Trinity College, Dublin, vol. 2, pp. 5 *et seq.*) in the case of *Tilia microphylla, Syringa vulgaris, Salix viminalis,* and Philadelphus sp. Similarly, Luise Birch-Hirschfeld (*Jahrb. f. wiss. Bot.*, Bd. 59, pp. 171 *et seq.*) has shown that a solution of lithium nitrate may be carried considerable distances downwards in the reversed transpiration stream of various trees, shrubs, and herbs.

Naturally the question obtrudes itself as to how a downward current of dissolved carbohydrates is produced in the wood which is also the normal channel of the upward transpiration current. The subject calls urgently for investigation, and it may not be out of place to mention some of the hypotheses which must be tested.

If it could be shown that the wood of the vascular bundles were divided longitudinally by more or less impermeable partitions into isolated tracheal strands, we might suppose that the tension developed in the water in some of these strands by transpiring cells, while raising the sap in these, might draw down solutions ejected by adjacent cells in neighbouring strands. No such vertical partitions have been described, unless the late summer wood or the vertical plates of parenchyma in the leaf veins and petioles be regarded as such. With such longitudinal partitions a continuous and contemporaneous upward and downward transport might be developed.

An intermittent downward flow might be explained if we could obtain evidence of a periodic or occasional development of permeability in the protoplasmic utricle of the transpiring cells. This might be developed in response to any stimulus, *e.g.* the mounting of tension in the adjacent sap above a certain limit.

The periodic mounting of tension with consequent contraction of the stem, which is indicated in the experiment on the potato plant quoted above, has been established by the elegant observations of Mallock (Proc. Roy. Soc., 1919, vol. 90, B, pp. 186–91) and of MacDougal ("Growth in Trees," Carnegie Institution of Washington, Washington, 1921). These latter show graphically the change of volume of the woody stem of forest trees corresponding to the diurnal period.

Again, the deposit of dew on the transpiring cells, in conjunction with a high tension, might determine a downward flow in the tracheæ, and, with suitable modification of the permeability of these cells, this downward stream might be charged with dissolved carbohydrates.

It is quite evident that the tension assumed here may be developed by temperature changes of the water in the woody tissues and by recovery from flexure just as well as by evaporation. That tension is really responsible is indicated by the experiments quoted above, and also by the fact that no transport occurs from cut leaves floating in water.

If the view that the longitudinal transport of organic substances takes place in the tracheæ is established, speculation naturally arises as to the function of the bast. While the form and arrangement of this tissue seem to preclude any important longitudinal transmission within it, its large peripheral surface and the area of its contact with the cambium and medullary rays seem to suit it for the transmission of organic substances in a radial direction. In this connection the medullary rays may have the function of discharging into, and extracting from, the tracheæ organic substances which are transmitted to and from them by the bast. The observations made by Atkins and one of us that the concentration of carbohydrates in the conducting tracts often diminishes from below upwards suggests that these substances may be extracted from the transpiration current in its upward movement (H. H. Dixon and W. R. G. Atkins, Notes from the Botanical School of Trinity College, Dublin, vol. 2, pp. 335 *et seq.*). The presence of starch in the medullary-ray cells in many plants at all times of the year suggests that the carbohydrates are fixed in these cells as starch. Solution by enzymes of this starch in response to an upward or a downward movement of the water in the tracheæ would provide a mechanism for the upward or downward transport of these substances in the transpiration stream.

It is hoped by experiments which are now in progress to throw some further light on this fundamental problem of plant physiology.

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Lunar Periodicity in Reproduction.

It is a common belief in many fish-markets around the Mediterranean and in other parts of the world that the amount of edible matter in sea-urchins and certain other invertebrates varies with the phases of the moon. The animals are said to be "full" when the moon is full and "empty" at new moon. This belief was recorded by Aristotle, Pliny, and other classical writers, and was stated by them to apply not only to sea-urchins, but also to oysters and other molluscs.

During the summers of 1920 and 1921 I made systematic examinations of the gonads of an Echinoid (*Diadema setasum*) at Suez with the object of testing the truth of the popular statement. I found the latter to be founded on fact to a surprising degree. There is a periodic reproductive cycle in this species of Echinoid which is correlated with the lunar period, the genital products being discharged into the sea at about each full moon during the breeding season. An examination of the testes and ovaries of a number of individuals between the first quarter and full moon shows the majority to be swollen and full of mature spermatozoa or eggs, while a lesser number are "spent," *i.e.* show evidence of having lately extruded their genital products. A week later the relative proportions are reversed. Some individuals have gonads still full of spermatozoa or eggs, but most are now "spent." Between the third quarter and the new moon all gonads are shrunken in size and contain nothing but developing spermatocytes or oocytes. From now onwards until the first quarter of the next moon these cells show progressive stages in development into spermatozoa and eggs which are to be spawned at about the time of full moon. This lunar cycle is repeated throughout the breeding season.

In seeking a causal connection between the reproductive rhythm and the lunar month an influence of the tides first suggests itself. But whereas there is a single reproductive cycle in each lunation, there are two spring and neap tidal periods, *i.e.* a double cycle. However, during the summer months at Suez the new moon spring tides have a greater range than those of the full moon, so that the maximum tidal range is attained only once during each lunar month. The higher and lower water at the new moon spring tides might conceivably react on the Echinoids by the different hydrostatic pressure (affecting, *e.g.*, the tension of dissolved gases) or by causing the animals to be at a greater or less distance than usual from the source of oxygen or of light. But the average excess tidal range at new moon spring tides over that at full moon spring tides during the period studied was only 58 cm. This small difference could scarcely affect the

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